Competition Between Alien Annual Grasses and Native Annual Plants in the Mojave Desert

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ABSTRACT.—Alien annual grasses in the genera *Bromus* and *Schismus* are widespread and abundant in the Mojave Desert, and negative correlations between these aliens and native annual plants suggest that competition may occur between them. Effects of competition were evaluated by thinning alien annual grass seedlings and measuring the responses of native annual plants at three sites in the central, southcentral and southwestern Mojave Desert during 2 y of contrasting plant productivity. Effects of *Bromus* and *Schismus* were evaluated separately in the microhabitat where each was most abundant, beneath the north side of creosote bushes (*Larrea tridentata*) for *Bromus* and in the open interspace between shrubs for *Schismus.* Thinning of *Bromus* and *Schismus* significantly increased density and biomass of native annuals at all three sites, only during a year of high annual plant productivity and species richness. Effects of thinning were greatest for *Amsinckia tesselata* and for a group of relatively uncommon native annuals. Thinning also significantly increased the density and biomass of the alien forb, *Erodium cicutarium.* These results show that alien annual grasses can compete with native annual plants and an alien forb in the Mojave Desert and that effects can vary among years.

INTRODUCTION

Alien plants can alter the structure of native plant communities. In the Mojave Desert, biomass of alien annual plants is negatively correlated with biomass and species richness of native annuals, even when potential covarying factors such as disturbance and soil nutrient levels are accounted for (Brooks, 1998). In particular, biomass of alien annual grasses is negatively correlated with that of native annuals. These observations suggest that alien annuals may affect the community structure of natives in this region, possibly through interspecific competition.

Two of the most widespread and abundant alien annual plant taxa in the Mojave Desert are the annual grasses *Bromus madritensis* ssp. *rubens* (hereafter called *Bromus rubens*) and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999). These alien grasses affect native desert annuals by promoting wildfires (Brooks, 1999a) and possibly by competing with them for limiting resources such as nitrogen (Brooks, 1998) and water (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). *Bromus rubens* is invasive in its Mediterranean home range and is considered a wildland weed in the Mojave Desert (Brooks, 2000a). It has been present in this region since the early 1900s, but appears to have significantly increased in dominance since the 1970s (Hunter, 1991). *Schismus* spp. (*Schismus arabicus* and *Schismus barbatus*) is not invasive in its Middle Eastern home range, but is considered a wildland weed in the Mojave Desert (Brooks, 2000b). *Schismus* spp. invaded this region during the 1940s and apparently became dominant by the 1950s (O.

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Clarke, pers. comm.). Two other alien annual grasses, *Bromus tectorum* and *Bromus trinii,* are locally abundant but not as widespread and common as *Bromus rubens* and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999).

Although competition has been shown to occur among native desert annuals (Went, 1949; Klikoff, 1966; Inouye *et al.*, 1980; Kadmon and Shmida, 1990; Pantastico-Caldas and Venable, 1993; Venable *et al.,* 1993), it has rarely been demonstrated between native and alien species (Sonoran Desert: Inouye *et al.*, 1980; Pake, 1993; Mojave Desert: Hunter, 1995). Competition between *Bromus rubens* and native annual plants was evaluated in the northern Mojave Desert by experimentally reducing its dominance by thinning and by applying a grass specific herbicide (Hunter, 1995). Although these treatments increased the average density, biomass and species richness of native annual plants, the results were not statistically significant, possibly because of insufficient sample sizes. Competition between *Schismus* and native annuals was reported in the Sonoran Desert where fecundity of *Schismus barbatus* was compared with fecundity of the native annuals *Plantago patagonica* and *Pectocarya recurvata* (Pake, 1993). At high levels of annual plant productivity, fecundity of *Schismus barbatus* was significantly higher than that of the native species, but results varied among productivity levels suggesting that the competitive hierarchies were variable. The competitive effects that dominant alien plants have on natives and the conditions where competition is most likely to occur need to be understood to effectively conserve and restore native plant communities.

The purpose of this study was to test the hypothesis that alien annual grasses in the genera *Bromus* and *Schismus* compete with native annual plants in the Mojave Desert. Competitive effects can be caused by a variety of mechanisms, including interference competition, exploitation competition, apparent competition and higher order interactions (Goldberg and Scheiner, 1993). The common characteristic of these mechanisms is that absolute abundances of plants are higher when and where abundances of their competitors are reduced. The net effect of all possible types of competition is documented in this study.

Competitive effects of alien annual grasses on native annual plants were evaluated by comparing plots that were thinned of alien grasses to unthinned reference plots. Effects were evaluated among three sites and between 2 y to evaluate spatial and temporal variation in competition. The competitive effects of *Bromus* and *Schismus* were evaluated in separate experiments because effects of aliens often vary among taxa (Lodge, 1993).

METHODS

Study sites.—Three individual 1 ha study sites were established in the central, southcentral and southwestern Mojave Desert (Rowlands *et al.*, 1982). The site within each region was located at least 25 m from dirt roads, 1 km from paved roads, 2 km from human habitations, on undeveloped land managed by the United States Department of the Interior, Bureau of Land Management. All sites had granitic soils from the early to middle Holocene which are typical of these regions of the Mojave Desert. Soils at the southwestern site were well drained, gravely, Randsburg sandy loams less than 30 cm deep over a granitic pediment (Valverde and Hill, 1981). Soil surveys were not available for the other two sites, but soils were of similar granitic sandy loam. Longterm rainfall patterns at each site were estimated by averaging the distance-weighted, monthly precipitation averages from the three closest National Oceanic and Atmospheric Administration weather stations (U.S. National Oceanographic and Atmospheric Association, 1995). Winter rainfall amounts were recorded every two weeks from October through April during this study using a single rain gauge at the center of each site.

All sites contained creosote bush scrub plant communities (Munz, 1968) dominated by

winter annual plants. Winter annuals germinate from September through December and remain as small vegetative tufts or rosettes until March or April when they rapidly grow, reproduce and die by May (Mulroy and Rundel, 1977). There are over 100 species of winter annuals compared to approximately 15 species of summer annuals in the Mojave Desert (Rowlands *et al.,* 1982). The dominant alien plants at all three sites were the winter annual grasses *Bromus rubens* and *Schismus* spp. and the forb *Erodium cicutarium.* The native winter annual grasses *Vulpia microstachys* and *Vulpia octoflora* were present at all sites, but were uncommon. Plant nomenclature followed Hickman (1993).

The central Mojave site was located south of Black and Opal mountains near Water Valley, San Bernardino County, California (35°07′30″N, 117°07′45″W) at 800 m elevation on a south facing alluvial bajada with 0–3% slope. Long-term average winter rainfall was 79 mm. The perennial plant community was dominated by *Larrea tridentata* and *Ambrosia dumosa,* but also included *Pleuraphis rigida* and *Achnatherum hymenoides.* No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and off highway vehicle (OHV) use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southcentral Mojave site was located at the northern edge of the Ord Mountains, San Bernardino County, California (34°41′30″N, 117°57′30″W) at 1100 m elevation on a northwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 78 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and OHV use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southwestern Mojave site was located at the southwest tip of the Rand Mountains in the Desert Tortoise Research Natural Area, Kern County, California (35°14′30″N, 117°51′15″W) at 870 m elevation on a southwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 104 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. This site was closed to OHV use in 1973 and livestock grazing in 1976 (U.S. Bureau of Land Management, 1980ab). Further descriptions of the southwestern Mojave site can be found in Brooks (1999b).

Thinning treatments.—Effects of competition were tested by thinning the seedlings of two dominant alien annual grass genera, *Bromus* and *Schismus,* at the beginning of the growing season and evaluating the effects of thinning on density and biomass of native annuals at the end of the growing season. The relative composition of *Bromus* seedlings that were thinned was estimated because the individual species were difficult to distinguish as seedlings. *Bromus* seedlings were composed of approximately 90% *Bromus rubens* and 10% *Bromus tectorum* and *Bromus trinii.* The relative composition of *Schismus* seedlings that were thinned could not be reliably estimated.

Bromus and *Schismus* seedlings were thinned in the microhabitat where each was most abundant (Samson, 1986; Brooks, 1998; Brooks 1999c) and therefore most likely to compete with natives. *Bromus* seedlings were thinned beneath the canopy on the north side of creosote bushes (*Larrea tridentata*) (beneath-canopy microhabitat). *Schismus* seedlings were thinned in the open space between the canopies of perennial shrubs and bunchgrasses (interspace microhabitat). Seedlings were thinned using forceps and scissors and disposed of away from the plots. All aboveground portions of living plants were removed, leaving the roots intact and the soil undisturbed. Thus, alien annual grass seedlings were not completely removed, but their overall rates of photosynthesis and consumption of nutrients were reduced compared to unthinned reference plots.

Thinning treatments began when seedlings emerged approximately two weeks after the

first and only cohort of annual plants germinated during each year. The time that the treatments began varied by two weeks among sites within each year. All treatments began in January, ended in February and consisted of an initial thinning followed by a second thinning two to three weeks later. In 1996, the average number (± 1 SE) of *Bromus* seedlings thinned per 500 cm² plot was 128 ± 14 and the average number of *Schismus* thinned was 29 ± 4. In 1997, the average number of *Bromus* seedlings thinned per plot was 253 ± 33 and the average number of *Schismus* thinned was 52 ± 12.

Thinning experiments of this type are commonly used to evaluate competition in situ within plant communities, but they have problems (Campbell *et al.,* 1991; Goldberg and Barton, 1992). One problem is that soil disturbance and root death of thinned plants can affect soil microbial processes and the amounts of mineral nutrients such as nitrogen (Wilson and Tilman, 1991; McLennan *et al.*, 1995). Thus, effects of thinning can be erroneously attributed to competitive release when they are actually a result of altered levels of soil nutrients. Another problem is that thinning effects can vary within years depending on the phenological stages of plant species when thinning is applied (Campbell *et al.*, 1991), and possibly among years depending on the productivity and species composition of annual plant seedlings. These potential confounding effects were evaluated in the current study by monitoring levels of nitrate and ammonium in the soil of thinned and reference plots, thinning during years when only one cohort of seedlings emerged, and documenting community biomass and species composition during each year.

Experimental and sampling design.—Experimental factors were replicated at 25 stations arranged in a 5×5 grid at 25 m intervals within each of the three study sites. At each station four contiguous 20×25 cm (500 cm²) experimental plots were placed end-to-end on their long axes in each of two microhabitats. For the *Bromus* thinning experiment, the experimental plots were placed in the beneath-canopy microhabitat of the closest creosote bush located in a random compass direction from each station. The four plots were oriented in an arc ($\sim 30°$) corresponding to the position of the beneath-canopy microhabitat. Beneath-canopy microhabitats were only used for creosote bushes with canopy diameters of at least 150 cm so the four experimental plots would fit completely within this microhabitat. For the *Schismus* thinning experiments, the experimental plots were placed in the closest interspace microhabitat located in a random compass direction >1 m from the creosote bush used for the beneath-canopy microhabitat at each station. The four plots were placed end to end in an arc of the same shape as described above for the beneath-canopy microhabitat. Individual experimental plots were randomly assigned a single level of each experimental factor, treatment (thinning and reference) and year (1996 and 1997). Hence, two plots served as thinning and reference plots during 1996 and two others served as thinning and reference plots during 1997. The total number of treatment plots was 600 (2 years $\times$ 2 treatments $\times$ 2 species(microhabitats) $\times$ 25 stations $\times$ 3 sites).

The responses of native annual plants to the thinning treatments were evaluated by collecting annual plant samples when winter annuals reached peak biomass and before they began to senesce. Samples were collected 10–18 April 1996 and 9–17 March 1997. Live annual plants were clipped at ground level within 10 x 20 cm sampling frames, counted by species, dried to a constant mass at 60 C and weighed to determine aboveground live dry biomass. Each sampling frame was centered within the 500 cm² experimental plots. Samples from the 2 y were considered repeated measures, because they were collected within 1 m of each other from the same microhabitat located within each station at each site.

Soil samples were collected from a random subset of six sampling frames in each of the two microhabitats after annual plants were harvested in March 1997. Samples were 8 cm diameter by 7 cm deep and were centered within the sampling frame. Soils were immedi-
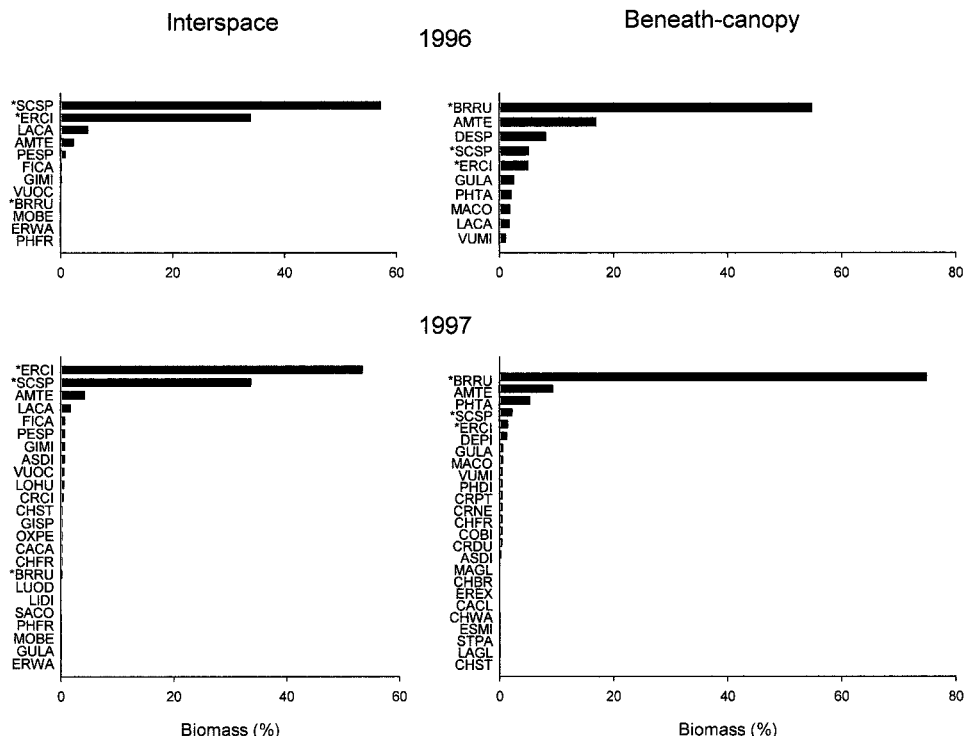
FIG. 1.—Percent biomass of annual plant species in interspace and beneath canopy microhabitats in 1996 and 1997. Species codes are defined in Appendix A; * = alien species

ately sieved (2 mm), stored in airtight plastic bags and analyzed by the University of California, Davis, Division of Agricultural and Natural Resources Analytical Laboratory.

Analysis of data.—Five dominant native annual plant taxa were evaluated individually, and the remaining less dominant native annuals were evaluated collectively as a group called "other natives" (n = 6 response variables). The dominant taxa had the highest density and biomass among natives within each microhabitat during both years at all sites, although their order of dominance varied between years (Fig. 1). The composition of the other natives group varied between microhabitats and between years. For the *Bromus* experiment, the response variables included *Amsinckia tesselata, Descurania pinnata, Malacothrix coulteri, Gullenia lasiophyllum, Phacelia tanacetifolia* and other natives. For the *Schismus* experiment, the response variables included *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pectocarya* spp. and other natives.

Treatment effects were evaluated separately for *Bromus* thinning in the beneath-canopy microhabitat and *Schismus* thinning in the interspace microhabitat. All treatment-by-site, treatment-by-sampling station and treatment-by-site-by-sampling station interactions were not significant (P > 0.250), so these terms were pooled in the final model (3 sites × 25 sampling stations = 75 spatial replicates) (Underwood, 1997). The final general linear model was balanced with two fixed factors, treatment nested within year. Data were transformed using square root (x + 0.5) for density and species richness and $\log_{10}$ (x + 1) for

biomass (Sokal and Rohlf, 1995). These transformations made the data more normally distributed and homoscedastic.

The data were analyzed in four steps. First, graphical plots were created displaying the average density and biomass of the dominant native and alien annual plant taxa in thinning and reference treatments during 1996 and 1997. Dominant alien plants were included to evaluate the effects of thinning on the alien grass taxa that were thinned, and to evaluate potential indirect effects of thinning on natives that may have been mediated through alien taxa that were not thinned (*e.g., Erodium cicutarium*). Second, repeated measures analysis of variance (ANOVA) was used to evaluate the significance of thinning treatments on total density and biomass of all native annual plants combined during each of the two years ($\alpha \leq 0.050$). Expected mean squares and significance tests were calculated using the GLM procedure and REPEATED statement of SAS statistical software (SAS Institute, 1985). Third, multivariate analysis of variance (MANOVA) was used to evaluate the significance of thinning treatments within each year on the density and biomass of five dominant, native, annual plant taxa plus the other natives group (6 response variables). MANOVA was used instead of multiple univariate ANOVAs because it does not require equal correlations among the response variables, it reduces the chance of type I errors that can occur with multiple univariate analyses, and it allows analyses of relationships among response variables (Scheiner, 1993; von Ende, 1993). Hotelling T^2 statistic was used to evaluate multivariate differences between thinning and reference plots (Morrison 1967). Degrees of freedom for the F-value of each MANOVA were p and $(N_1 + N_2 + p - 1)$, where $p = 6$ (response variables) and $N_1 = N_2 = 75$ (replicates). Standardized canonical coefficients and graphical plots were used to evalute the relative effect of thinning treatments on each response variable. Expected mean squares, significance tests, and standardized canonical coefficients were calculated using the GLM procedure and the MANOVA statement with the CANONICAL option (SAS, 1988). This procedure produced values of Wilks' λ, from which the Hotelling T^2 statistic was calculated using the formula: $T^2 = (n - 1) (1 - \lambda/\lambda)$ (Khattree and Naik 1995). Fourth, the significance of the six response variables used in each MANOVA were evaluated individually using ANOVA and bonferroni corrected type I error rates ($P \leq 0.05/6$ tests $= 0.0083$) (Sokal and Rohlf, 1995).

RESULTS

The amount and temporal distribution of winter (Oct.–Apr.) rainfall was similar at the three study sites, but differed between years during this study. In 1995–1996, winter rainfall averaged 94% of average (82 mm) and occurred in small increments throughout the winter. In 1996–1997 rainfall averaged 77% of average (67 mm), but occurred mostly in December when rainfall was 307% of average for that month (46 mm). This high December rainfall stimulated mass germination of annual plants which resulted in high biomass and species richness of annual plants during spring 1997. In the interspace microhabitat, amounts were higher in 1997 than 1996 for average (± 1 SE) annual biomass (1.05 ± 0.11 vs. 0.32 ± 0.15 g/200 cm^2) and species richness (6.78 ± 0.32 vs. 1.77 ± 0.10 species/200 cm^2). In the beneath-canopy microhabitat, amounts were also higher during 1997 than 1996 for average annual plant biomass (4.21 ± 0.40 vs. 0.12 ± 0.02 g/200 cm^2) and species richness (8.06 ± 0.35 vs. 1.79 ± 0.08 species/200 cm^2). Species composition also differed between years, with many more native species present in 1997 than 1996 (Fig. 1). Forty three species of annual plants were collected in this study (Appendix A), three of which were aliens which composed the majority of the total community biomass (Fig. 1).

Thinning treatments did not affect the amount of nitrate or ammonium present in the soil at the time annual plants were collected on 9–17 March 1997. In the beneath-canopy
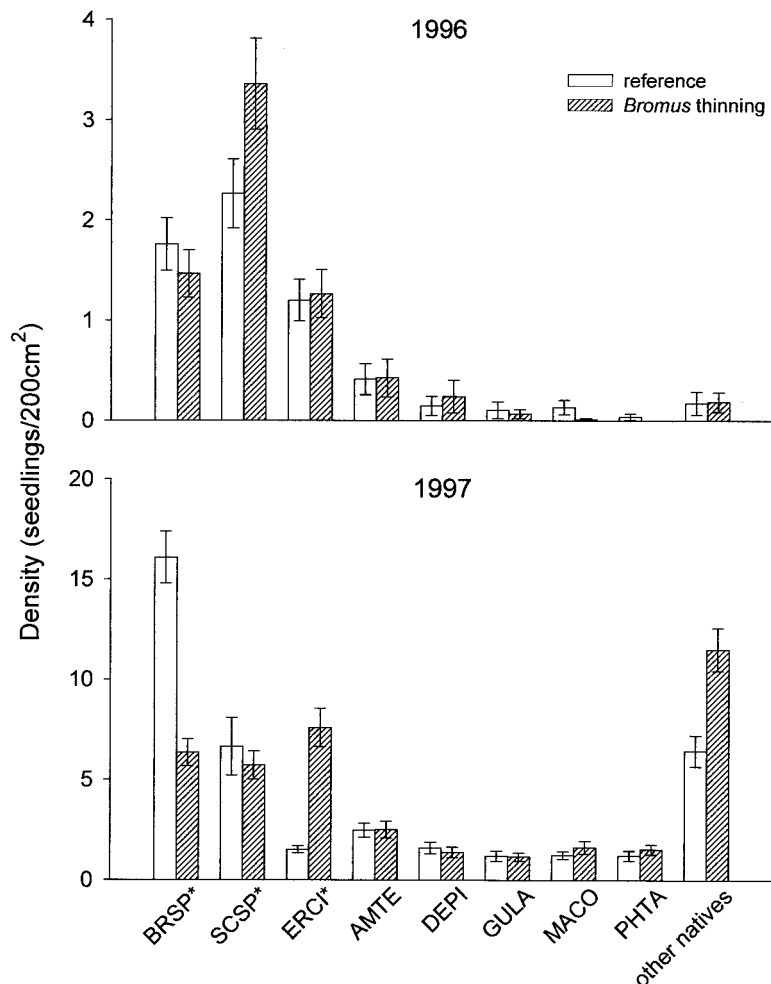
FIG. 2.—Effects of *Bromus* thinning on the density of annual plants in the beneath canopy micro-habitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in Appendix A; * = alien species

microhabitat, average (±1 SE) nitrate levels were 10.1 ± 1.1 ppm in treatment plots and 11.2 ± 0.9 ppm in reference plots, and ammonium levels were 3.4 ± 0.8 ppm in treatment plots and 3.7 ± 0.7 ppm in reference plots. In the interspace microhabitat, average nitrate levels were 4.8 ± 0.3 ppm in treatment plots and 4.9 ± 0.2 ppm in reference plots and ammonium levels were 1.1 ± 0.1 ppm in treatment plots and 1.0 ± 0.2 ppm in reference plots.

Effects of Bromus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Bromus* in treatment compared to reference plots (Figs. 2, 3). In 1996 *Bromus* density was 17% and biomass was 4% lower in treatment than reference plots. In
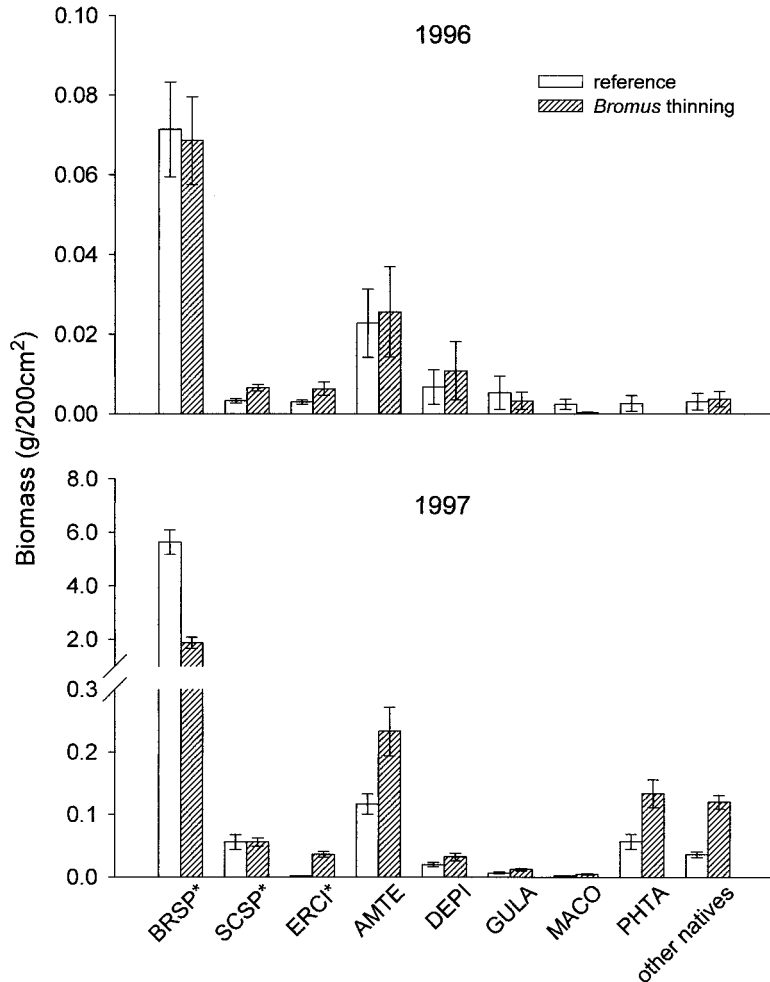
FIG. 3.—Effects of *Bromus* thinning on the biomass of annual plants in the beneath canopy micro-habitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in appendix A; * = alien species

1997, *Bromus* density was 61% and biomass was 67% lower in treatment than reference plots.

Thinning *Bromus* seedlings significantly affected the total density ($F_{1, 148}$ = 8.53, P = 0.004) and biomass ($F_{1, 148}$ = 22.57, P < 0.001) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions for density ($F_{1, 148}$ = 12.25, P = 0.001), and biomass ($F_{1, 148}$ = 35.15, P < 0.001). Density and biomass of native annuals was significantly affected by thinning *Bromus* in 1997 ($F_{1, 148}$ = 10.89, P = 0.001 and $F_{1, 148}$ = 32.58, P < 0.001 respectively), but not in 1996 ($F_{1, 148}$ = 0.03, P = 0.865 and $F_{1, 148}$ = 0.01, P = 0.980 respectively). Density of natives (seedlings/

TABLE 1.—MANOVA of the effects of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pecto-carya* spp. and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	6.19	1.02	6, 143	0.412
Biomass	6.14	1.03	6, 143	0.407
1997				
Density	14.53	2.58	6, 143	0.021
Biomass	46.75	10.90	6, 143	<0.001

200 cm^2 ±1 SE) was 19.61 ± 1.43 on *Bromus*-thinned plots compared to 14.21 ± 0.88 on reference plots in 1997, and 0.93 ± 0.36 on thinned plots compared to 1.01 ± 0.29 on reference plots in 1996. Biomass of natives (g/200 cm^2) was 0.06 ± 0.02 on thinned plots compared to 0.05 ± 0.02 on reference plots in 1997, and 0.54 ± 0.06 on thinned plots compared to 0.24 ± 0.03 on references plots in 1996.

The multivariate effect of *Bromus* thinning on the six dominant native taxa was significant in 1997 but not 1996 (Table 1), although not all individual taxa were affected equally (Figs. 2, 3). For density, standardized canonical coefficients indicated that the other natives category was the group most affected by thinning treatments in 1997 (Table 2; $F_{1, 148} = 14.50$, $P < 0.001$). For biomass, other natives ($F_{1, 148} = 48.49$, $P < 0.001$) and *Amsinckia tesselata* ($F_{1, 148} = 7.63$, $P < 0.001$) were most affected by treatments.

Bromus thinning did not significantly reduce the density or biomass of *Schismus*, but did significantly reduce density and biomass of a third dominant alien, *Erodium cicutarium*, during 1997 (Figs. 2, 3). Density of *Erodium cicutarium* was significantly higher on thinned than reference plots in 1997 ($F_{1, 148} = 39.50$, $P < 0.001$) but not 1996 ($F_{1, 148} = 0.40$, $P = 0.884$), and biomass of *Erodium cicutarium* was significantly higher on thinned plots during 1997 ($F_{1, 148} = 57.11$, $P < 0.001$) but not 1996 ($F_{1, 148} = 3.76$, $P = 0.054$).

Effects of Schismus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Schismus* in treatment compared to reference plots (Figs. 4, 5). In 1996, *Schismus* density was 81% and biomass was 65% lower in treatment than reference plots. In 1997, *Schismus* density was 90% and biomass was 83% lower in treatment than reference plots.

Thinning *Schismus* seedlings significantly affected the total density ($F_{1, 148} = 14.73$, $P < 0.001$) and biomass ($F_{1, 148} = 8.86$, $P = 0.003$) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions

TABLE 2.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of native annual plant taxa during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

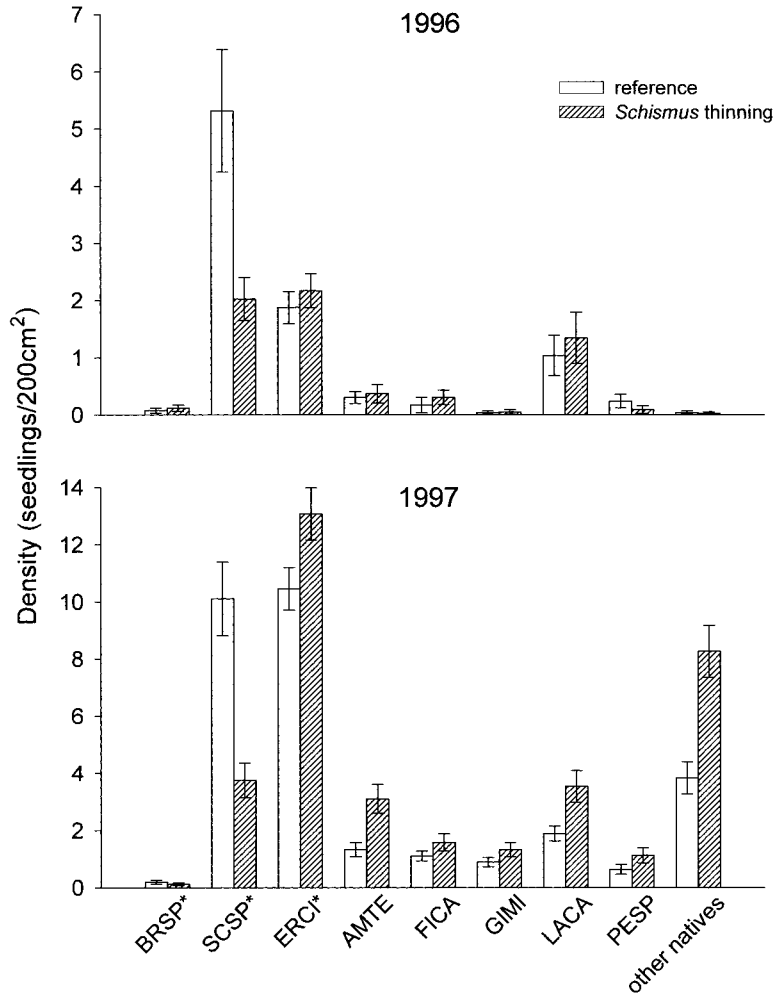|	AMTE	DEPI	GULA	MACO	PHTA	Other natives
Density	0.205	−0.202	−0.160	0.150	0.039	1.004
Biomass	0.462	0.072	0.217	0.263	0.173	0.850

FIG. 4.—Effects of *Schismus* thinning on the density of annual plants in the beneath canopy micro-habitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

for density ($F_{1, 148}$ = 17.41, P < 0.001), and biomass ($F_{1, 148}$ = 15.42, P < 0.001). Density and biomass of native annuals were significantly affected by thinning in 1997 ($F_{1, 148}$ = 23.24, P < 0.001 and $F_{1, 148}$ = 14.05, P < 0.001), but not in 1996 ($F_{1, 148}$ = 0.07, P = 0.793 and $F_{1, 148}$ = 0.64, P = 0.426). Density of natives (seedlings/200 cm²) was 19.43 ± 1.40 on *Schismus*-thinned plots compared to 9.89 ± 0.75 on reference plots in 1997 and 2.12 ± 0.50 on thinned plots compared to 1.84 ± 0.40 on references plots in 1996. Biomass of natives (g/200 cm²) was 0.18 ± 0.2 on thinned plots compared to 0.08 ± 0.01 on reference plots in 1997, and 0.03 ± 0.01 on thinned plots compared to 0.03 ± 0.01 on references plots in 1996.
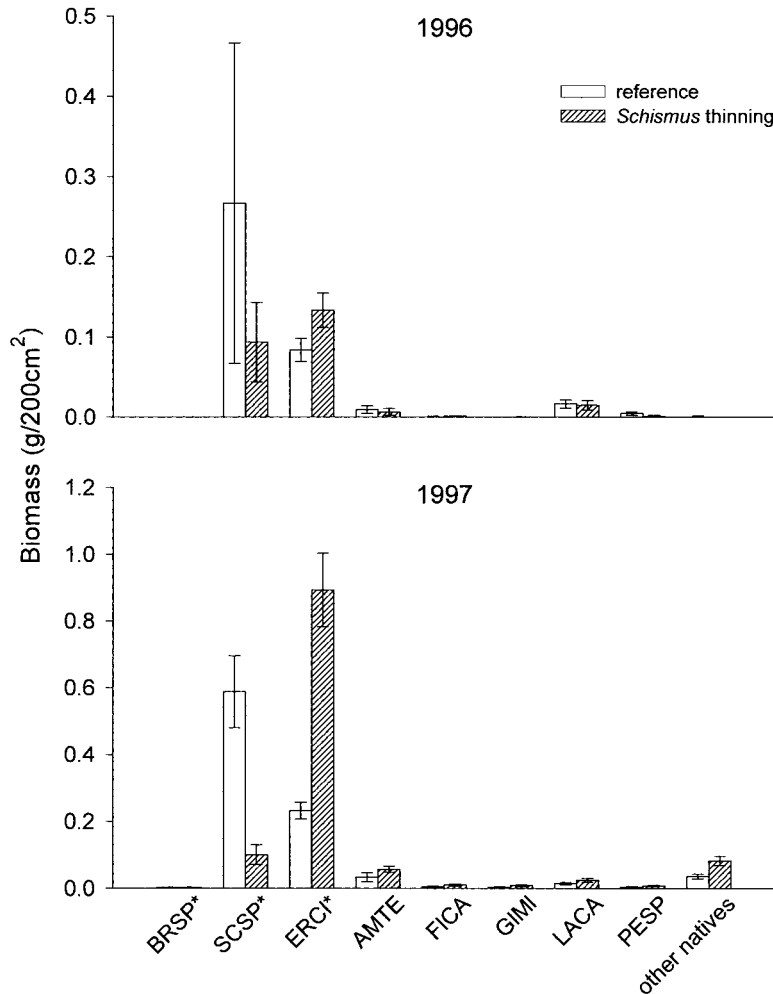
FIG. 5.—Effects of *Schismus* thinning on the biomass of annual plants in the beneath canopy micro-habitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

The multivariate effect of *Schismus* thinning on dominant native taxa was also significant in 1997 but not 1996 (Table 3), although not all individual taxa were affected the same (Figs. 4, 5). Standardized canonical coefficients of density indicated that *Amsinckia tesselata* ($F_{1, 148}$ = 7.45, P = 0.007) and other natives ($F_{1, 148}$ = 12.63, P = 0.001) were the native taxa most affected by thinning treatments in 1997 (Table 4). Biomass of other natives was most affected by treatments in 1997 ($F_{1, 148}$ = 9.63, P = 0.002).

Schismus thinning did not significantly affect density or biomass of *Bromus* because *Bromus* was uncommon in the interspace microhabitat (Figs. 4, 5). After *Schismus* thinning, *Erodium cicutarium* significantly increased in density during 1997 ($F_{1, 148}$ = 4.98, P = 0.027)

TABLE 3.—MANOVA of the effects of *Schismus* thinning in the interspace microhabitat on the density and biomass of *Amsinckia tesselata, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	2.80	0.46	6, 143	0.840
Biomass	4.85	0.86	6, 143	0.570
1997				
Density	20.34	3.77	6, 143	<0.001
Biomass	14.50	2.57	6, 143	<0.001

but not 1996 ($F_{1, 148}$ = 0.53, P = 0.469), and in biomass during 1997 ($F_{1, 148}$ = 39.99, P < 0.001) but not 1996 ($F_{1, 148}$ = 3.38, P = 0.068).

Other observations.—Native annual plant seedlings in reference plots began to senesce approximately 2 wk earlier than those in thinned plots during 1997. Withering shoot tissue marked the onset of senescence. Many of these senescent seedlings died before they produced seeds and were not included in the samples of live annual plants collected in March 1997. The differential senescence of annual plants between treatments was not observed in 1996.

DISCUSSION

The results of this study support the hypothesis that competition occurs between alien annual grasses and native annual plants in the Mojave Desert. Thinning of alien annual grasses increased total density and biomass of native annual plants, but significantly affected only one of the five most dominant native species. This species, *Amsinckia tesselata,* is a common forb in disturbed areas of the Mojave Desert (Hickman, 1993). The results of this study should be interpreted cautiously because it was designed to evaluate the net effects of competition. Possible indirect effects between and among alien and native species prevent definitive conclusions regarding the mechanisms of competition. Evidence is discussed below that implicates certain mechanisms that are proposed as hypotheses for further study.

Thinning treatments can produce unwanted effects that complicate the interpretation of plant competition experiments (Campbell *et al.*, 1991; Goldberg and Barton, 1992), but these confounding effects were not detected in the current study. For example, thinning treatments did not affect levels of available nitrogen in the soil, indicating that thinning did not cause changes in soil fertility. In addition, the soil was left undisturbed on thinned plots, so surface disturbance was not a factor causing differences between treatment and

TABLE 4.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Schismus* thinning in the interspace microhabitat on the density and biomass of native annual plants during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

	AMTE	FICA	GIMI	LACA	PESP	Other natives
Density	0.619	0.058	0.256	0.280	0.129	0.612
Biomass	0.470	0.312	0.239	0.140	0.061	0.633

reference plots. Alien annual grasses can also affect natives by altering fire regimes, bio-geochemical cycles and rates of leaf litter accumulation (D'Antonio and Vitousek, 1992), but these effects should not occur within the four month interval of this experiment during each year. Thus, it seems reasonable to conclude that the effects of thinning were attrib-utable to reduced net competition from alien annual grasses.

The mechanisms by which annual plants compete with each other result in different outcomes with respect to density and biomass. Densities of annual plants can either be affected by germination inhibition or by post-germination competition for limiting resourc-es in the deserts of southwestern North America (Went, 1949; Juhren et al., 1956; Inouye, 1980; Inouye et al., 1980). In contrast, biomass of annual plants is affected primarily by post-germination competition (Inouye, 1991). In the current study there was only one co-hort of annual plants that germinated each year and thinning treatments were applied after these seedlings germinated, so the effects of thinning should have been caused by post-germination competition.

Accelerated senescence of native annual plants in thinned compared to reference plots suggest that alien annual grasses competed with native seedlings for water and mineral nutrients as these nutrients became less abundant at the end of the growing season. *Bromus rubens, Schismus* spp. and *Erodium cicutarium* can assimilate nitrogen faster than native annuals in the central, southern and western Mojave Desert (Brooks, 1998), and *Bromus tectorum* can acquire water more rapidly than native annuals in the Great Basin desert (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). Nitrogen and water are consid-ered to be the two primary factors that limit plant growth in the Mojave Desert (Rundel and Gibson, 1996). Hence, the competitive superiority of some alien annuals may be linked to competition for these nutrients. Experimental manipulations of seedling densities and nutrient levels are required to test this hypothesis.

Effects of thinning were similar at all three study sites and significant only during a year of overall high productivity, suggesting that competition of aliens with natives may be wide-spread but varies among years. However, these hypotheses require additional testing because site and year were fixed effects in this study. Moreover, the sites were all in plant commu-nities dominated by the widespread and common perennial shrub *Larrea tridentata,* and interactions between alien and native annuals may be different in other plant communities. In addition, the 2 yr studied differed in biomass, species richness and species composition of annual plants, all factors that may affect competitive hierarchies. Studies documenting the net effects of competition should not be generalized beyond their spatial and temporal ranges, because the multiple mechanisms that influence these net effects can vary in space and time (Goldberg and Scheiner, 1993).

Thinning treatments increased the density and biomass of *Erodium cicutarium,* a wide-spread and abundant alien annual forb. This species has been present in southwestern North America since the 1600s (Mensing and Byrne, 1999), in contrast to most other exotic annuals that invaded during the late 1800s and early 1900s (Heady, 1988). The increase in density and biomass of *E. cicutarium* was approximately equal to the reduction of alien annual grass abundance on thinned plots, resulting in no net change in the proportional density and biomass of aliens (Brooks, 1998). Because the density and biomass of native annual plants increased despite similar increases in *E. cicutarium,* competition between them does not appear to have been significant. However, other evidence suggests *E. cicu-tarium* may compete with native annuals, based on negative correlations between their abundances in the Mojave (Brooks, 1998) and Sonoran Deserts (Inouye et al., 1980). Tests of the relationships between *E. cicutarium* and native annuals are required to draw any reliable conclusions about their competitive relationships.

Bromus and *Schismus* may compete with different subsets of the native annual plant community, based on their respective dominance of the beneath-canopy and interspace microhabitats and because thinning of these taxa in the microhabitat where they were each uncommon did not affect native annual plants (Brooks, 1998). Because many native annuals display preferences for one or the other of these microhabitats (Shreve, 1931; Went, 1942; Muller, 1953; Halvorson and Patten,1975; Shmida and Whittaker, 1981), *Bromus* and *Schismus* may compete with different suites of annual plant species. However, there are areas in the Mojave Desert where *Bromus* density and biomass is high across the landscape in both microhabitats (Brooks, 1998), and in these areas *Bromus* may compete with a wider range of annual plants than was observed in the current study.

The composition of annual plant communities in the Mojave Desert can vary greatly among seasons and germination cohorts (Jennings, 1993; Burk, 1982), and the results of the current study may have differed given a different suite of annual plant seedlings. This study focused on winter-germinating annual plants that grew together in a single germination cohort during each of two years. It is unknown if the effects of thinning would have been different had a second cohort of annual plants germinated after the thinning treatments were applied each year. It is also unknown if these alien winter annuals compete with native summer annuals that grow from late winter through early summer. If alien winter annuals use large amounts of soil nutrients during winter and spring, then they may affect summer annuals by reducing the amounts of nutrients available during spring and summer. This hypothesis requires testing, especially in the eastern part of the Mojave Desert where summer annuals are most abundant (Rowlands *et al.*, 1982).

This study demonstrates that alien annual grasses can significantly affect the density and biomass of native annual plant seedlings. Years of competition from these grasses may reduce the seed banks of native annuals, possibly causing fundamental changes in annual plant community structure and food web dynamics. The results also highlight the need to evaluate the effects of all dominant alien taxa, because aliens such as *Erodium cicutarium* may increase in dominance when alien annual grasses are removed. This conclusion is especially important to keep in mind when implementing management practices designed to minimize the dominance of individual species of alien annual plants.

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APPENDIX A.—Annual plants collected April 1996 and March 1997 at the DTNA

Amsinckia tesselata	AMTS	NF[1]	*Gilia minor*	GIMI	NF
Astragalus didymocarpus	ASDI	NF	*Gilia* species	GISP	NF
Bromus rubens	BRRU	AG	*Guillenia lasiophylla*	GULA	NF
Bromus species	BRSP	AG	*Lasthenia californica*	LACA	NF
Bromus tectorum	BRTE	AG	*Layia glandulosa*	LAGL	NF
Bromus trinii	BRTR	AG	*Linanthus dichotomus*	LIDI	NF
Camissonia campestris	CACA	NF	*Lotus humistratus*	LOHU	NF
Camissonia claviformis	CACL	NF	*Lupinus odoratus*	LUOD	NF
Chenactis fremontii	CHFR	NF	*Malacothrix coulteri*	MACO	NF
Chenactis steviodes	CHST	NF	*Malacothrix glabrata*	MAGL	NF
Chorizanthe brevicornu	CHBR	NF	*Monoptillon belliforme*	MOBE	NF
Chorizanthe watsonii	CHWA	NF	*Oxytheca perfoliata*	OXPE	NF
Coreopsis bigelovii	COBI	NF	*Pectocarya* species	PESP	NF
Crypthantha circumcissa	CRCI	NF	*Phacelia distans*	PHDI	NF
Crypthantha dumetorum	CRDU	NF	*Phacelia fremontii*	PHFR	NF
Crypthantha nevadensis	CRNE	NF	*Phacelia tanacetifolia*	PHTA	NF
Crypthantha pterocarya	CRPT	NF	*Salvia columbariae*	SACO	NF
Descurainia pinnata	DEPI	NF	*Schismus* species	SCSP	AG
Eremalche exilis	EREX	NF	*Schismus arabicus*	SCAR	AG
Eriophyllum wallacei	ERWA	NF	*Schismus barbatus*	SCBA	AG
Erodium cicutarium	ERCI	AF	*Stephanomeria parryi*	STPA	NF
Escholtzia minutiflora	ESMI	NF	*Vulpia microstachys*	VUMI	NG
Filago californica	FICA	NF	*Vulpia octoflora*	VUOC	NG

[1] AF = alien forb, AG = alien grass, NF = native forb, NG = native grass